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DIFFERENTIAL RANGE EXPANSION AND POPULATION GROWTH OF BULBULS IN HAWAII

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The Red-whiskered Bulbul (*Pycnonotus jocosus*) and the Red-vented Bulbul (*P. cafer bengalensis*) on Oahu, Hawaii, present a unique natural experiment in colonization rates. Both species were introduced on Oahu in the mid-1960s and are currently undergoing rapid population growth; however, they differ markedly in rates of range expansion. Van Riper et al. (1979) reviewed the range and population growth of the two species through 1977 and found the red-whiskered restricted to a small area in central Honolulu while the red-vented was distributed throughout lower elevation habitats in the southeast quarter of Oahu. The objectives of our study were: (1) to document continued range expansion and population growth by both species; and (2) to determine if differences in their rates of range expansion could be attributed to differing rates of population growth or differences in habitat selection. Here we report on a marked range expansion by the Red-vented Bulbul and continued rapid population growth by both species and suggest several hypotheses (currently under investigation) to explain the marked differences in distribution and habitat selection between the two species.

Red-whiskered and Red-vented bulbuls were introduced to Oahu without legal authorization in 1965 and 1966, respectively (Berger 1975, Williams 1983). Both species are native to India where they inhabit gardens, scrub, second growth, forest edges, and agricultural areas (Ali and Ripley 1971). They are similar in their morphology and ecology, including nesting and feeding habits (Ali and Ripley 1971). Both species appear preadapted for living in the residential lowlands of Oahu, many areas of which are replete with exotic fruit-bearing trees (Neal 1965).

Bulbuls have demonstrated the ability to colonize after being introduced in a number of temperate, tropical, and subtropical habitats. The red-whiskered is established in southeastern Australia (Long 1968), Mauritius (Long 1981), California (Hardy 1973), and Florida (Carleton and Owre 1975), while the red-vented is found in Fiji (Watling 1978), Tahiti (Bruner 1979), Tonga (Dhondt 1976a), Western Samoa (Dhondt 1976b), and southeastern Australia (Slater 1974). In most of these areas, they are considered pest species due to agricultural crop damage or as vectors for the dispersal of weedy plant species (Watling 1977). For these reasons,

the ecology, distribution, and population growth of the bulbuls in Hawaii are of both scientific and practical interest.

METHODS

We conducted an intensive survey (134 h of observation) from July 1981–February 1982, to document the current distribution of bulbuls on Oahu and conducted periodic surveys (46 h) through the remainder of 1982 to document any subsequent range expansion. We concentrated our surveys in areas below 200 m elevation along Oahu's coastal perimeter and central valley in residential, forest, and agricultural lands. We made some observations in second growth and native forests above 200 m. We recorded time (in min) at each survey location from the start of observations until the first bulbul of each species was detected. Elapsed observation time until detection was assumed in this study to reflect relative abundances. Elapsed observation times shown in Figs. 1 and 2 are average values, as data were collected more than once (range 2–6) at each location.

We examined population growth with data from the Hawaii Audubon Society's annual Christimas Bird Counts for the Honolulu area (Pyle 1965–1982). The Honolulu Count circle covers 456 km^2, including and extending beyond the introduction sites for both species. In order to standardize count results over the years 1965–1982, total number of bulbuls observed each year (by species) was divided by total party hours for that same year. As population growth is typically exponential, natural log transformations were performed on standardized population values for the Red-whiskered Bulbul from 1974–1982, and for the Red-vented Bulbul from 1968–1982, as these periods represent continuous growth intervals for these species. Population growth rates (regression coefficients) were examined for homogeneity using Homogeneity of Slopes model ANOVA (SAS 1982).

We examined distributional patterns of bulbuls in residential Honolulu throughout Manoa and Nuuanu valleys where both species were found in the highest concentrations. We started transects (5.0 km in length) in the upper valleys and extended them down past the valley mouths such that the upper half of the transect in each valley was located at higher elevations and received greater rainfall than did the lower half. Each transect was subdivided into 100-m segments, giving 50 segments per transect. Data were collected monthly from each transect with numbers of either species recorded for every 100-m segment. Odd-numbered segments were censused during odd-numbered months and even-numbered segments during even-numbered months. All observations were made during the first 3.5 h after sunrise. Thus, data were recorded for twenty-five, 100-m segments on each transect each month. Transect data were anlysed using Chi-square procedures to test within species differences in number of birds observed in the upper and lower halves of each transect (Little and Hills 1978). Significant differences ($P < 0.05$) were assumed to reflect habitat preferences for wet exotic residential habitat (upper half of transect) or dry exotic residential habitat (lower half of transect).

RESULTS

The distribution of the Red-whiskered Bulbul on Oahu is restricted to the central Honolulu area where there are two known introduction sites (Fig. 1) (Williams 1983). Red-whiskereds were found in low concentrations throughout most of their Oahu range. Highest concentrations were observed in residential areas in the upper portions of Manoa and Nuuanu valleys. Results from our intensive survey in 1981 and early 1982, showed a distribution almost identical to 1977 (Fig. 1). Periodic surveys through-

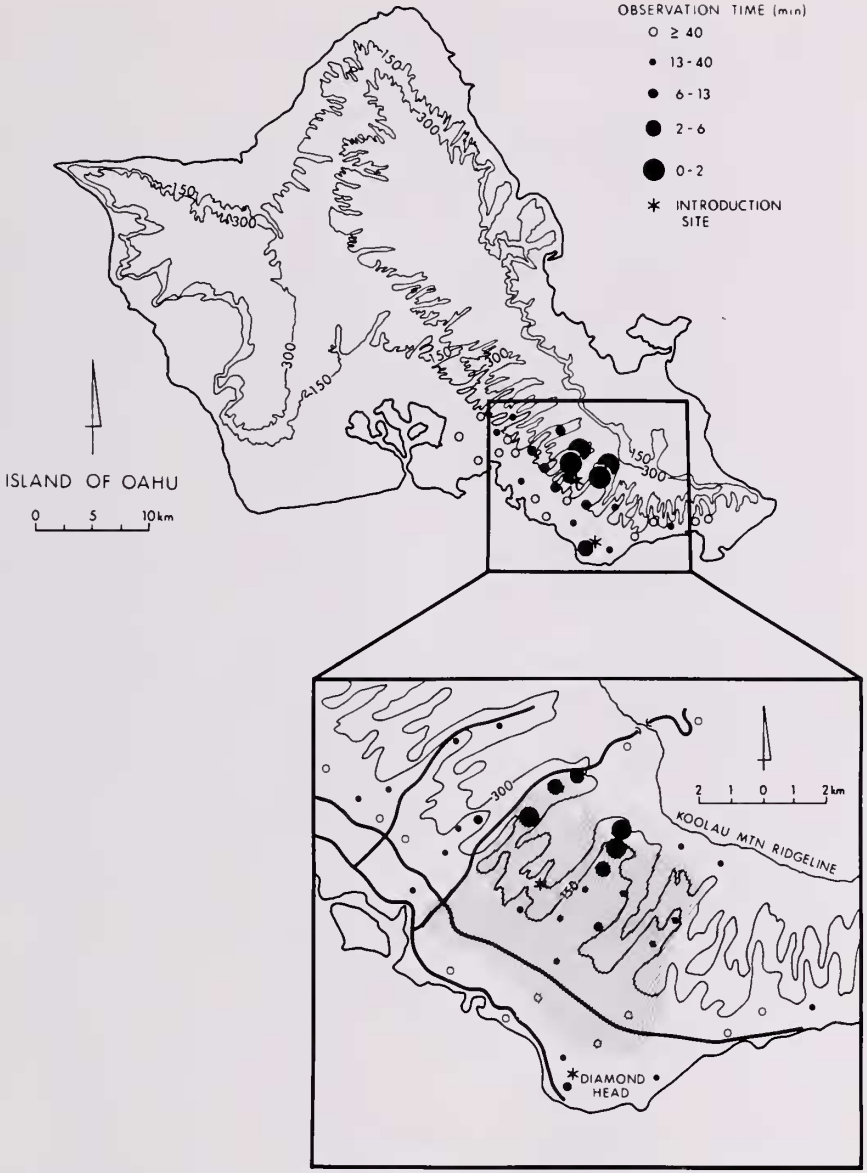

FIG. 1. Distribution and abundance of Red-whiskered Bulbuls on Oahu and in central Honolulu (inset map) as of December 1982. Open and closed circles indicate absence or presence of bulbuls, respectively. The larger the circle, the greater the relative abundance and the shorter the elapsed observation time. Data values on upper map are summary values, whereas values on inset map are actual data values from each location. Shaded section denotes 1977 distribution as reported by van Riper et al. (1979). Contour lines depict elevation in meters.

out the remainder of 1982 defined a larger distribution; one in which red-whiskered densities were quite low in areas lying outside the limits of the 1977 distribution.

In contrast to the limited distribution of the red-whiskered, we observed red-venteds at most lower elevations (Fig. 2). In 1977, the red-vented was restricted to the southeast quarter of Oahu, a distribution that encompassed the locations where it was first observed on Oahu in 1966–1967 (Williams 1983). The 1981–1982 survey revealed an absence of Red-vented Bulbuls on the western coast of Oahu. In August 1982, we discovered a small group in the lowland central portion of Makaha Valley. Since that time, we have made additional observations of this species along the western coast, although the birds are present in very low numbers. Numbers of red-venteds increased moving inland from the coast (Fig. 2 inset), reaching their highest levels in mid-elevation (100–200 m) portions of Honolulu's residential areas. They decreased in upper residential areas and wet exotic forest at elevations above 200 m.

We tested the hypothesis that the differences in distributions between the red-whiskered and the red-vented might be attributable to differential rates of population growth. The red-whiskered was first recorded in the 1967 Honolulu Area Christmas Bird Count and the red-vented in the 1968 count. Population growth through 1982 for both species is shown in Fig. 3. Population growth rates (regression coefficients) were 0.493 for the red-whiskered and 0.383 for the red-vented. Since the data were logarithmically transformed, these rates represent population doubling times of 1.4 and 1.8 years, respectively. Population growth rates were tested for homogeneity and there was no significant difference ($P > 0.05$).

To test for differences in habitat preference between the two species, we examined distributional patterns of bulbuls in residential Honolulu using monthly transet censuses over a 12-month period (Table 1). Red-whiskered Bulbuls were counted in significantly greater numbers ($P < 0.05$) in the upper half of Manoa Valley during 9 of 12 months of observations and in the upper half of Nuuanu Valley during 10 of 12 months. Significant differences were not detected for either species in Manoa Valley in November or December of 1982 during the non-breeding period for both species. By contrast, the red-vented occurred in significantly greater numbers ($P < 0.05$) in the lower half of Manoa Valley during 9 of 12 months. Red-vented distribution in Nuuanu was not significantly different ($P > 0.05$) in 11 of 12 months. Only in February 1983, were significantly more individuals ($P < 0.05$) detected in the lower half of the transect. Comparisons between Manoa and Nuuanu showed approximately equal numbers of red-venteds in the upper half of each transect (279 and 276

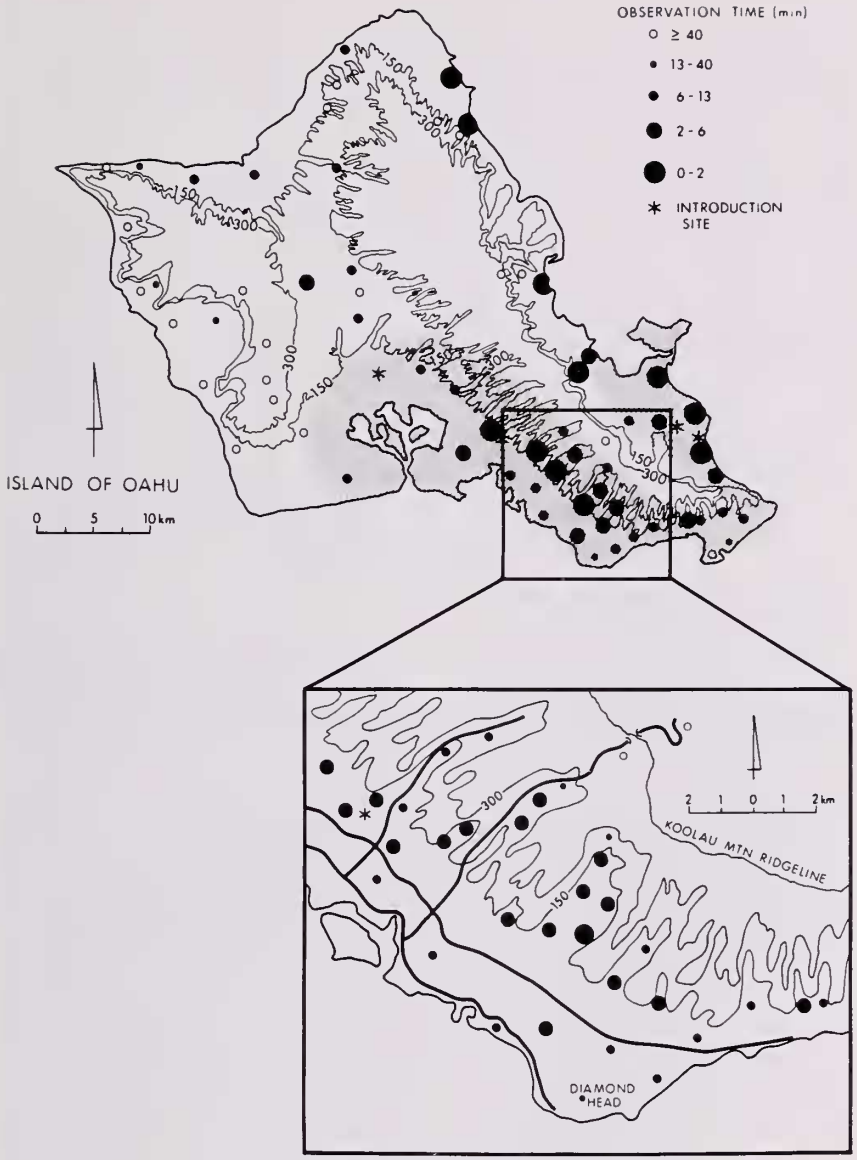

FIG. 2. Distribution and abundance of Red-vented Bulbuls on Oahu and in central Honolulu (inset map) as of December 1982 (symbols as in Fig. 1).

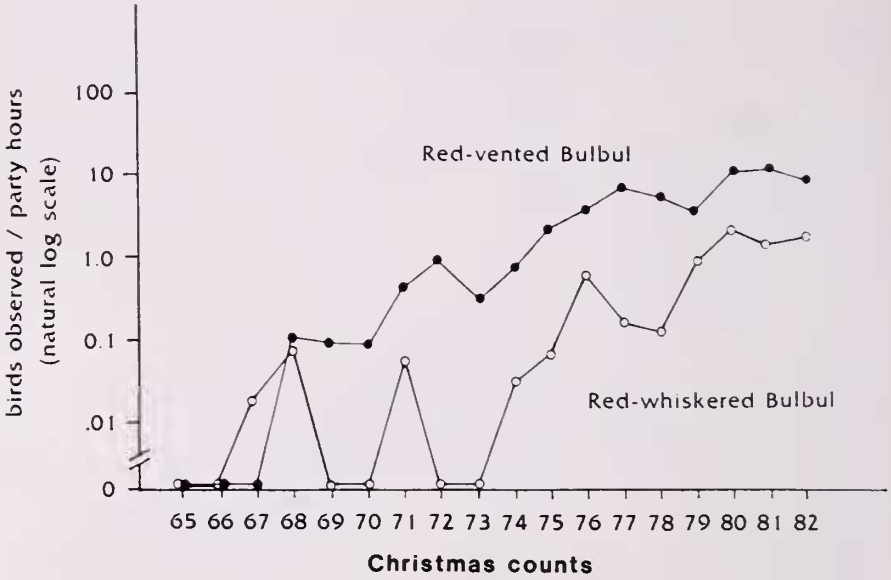

FIG. 3. Population growth of bulbuls on Oahu, 1965–1982. Data from Honolulu Christmas Bird Counts (Pyle 1965–1982).

birds, respectively), yet twice as many in the lower half of Manoa (546) as Nuuanu (268) ($\chi^2 = 86.4$, df = 1, $P \leq 0.05$).

DISCUSSION

As described above, we were intrigued by differences in range expansion rates and distribution of the two species. We hypothesized that the red-vented had a much higher rate of population growth than the red-whiskered, and that as the population grew, dispersal and subsequent range expansion accounted for its more extensive distribution. This hypothesis was tested using data from the Honolulu Area Christmas Bird Counts and was rejected by two results. First, the regression coefficients representing rates of population increase for the red-whiskereds and red-venteds did not differ significantly. Second, from 1977–1982, the red-vented approximately tripled its range on Oahu while the red-whiskered maintained a distribution similar to that defined in 1977 by van Riper et al. (1979). Therefore, it appears that differences in distribution and rate of range expansion between the two bulbuls cannot be ascribed to differences in population growth rates.

Differences in the distributions of the Red-whiskered Bulbul and the Red-vented Bulbul on Oahu suggest that they may be selecting differing habitats. In India, these two species have demonstrated habitat parti-

TABLE 1

NUMBERS OF BULBULS OBSERVED IN UPPER (U) AND LOWER (L) HALVES OF TRANSECTS IN MANOA AND NUUANU VALLEYS, OAHU, JUNE 1982–MAY 1983

	Months											
	1982							1983				
	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Manoa Valley												
Red-whiskered	U32*	47*	34*	56*	34*	15	13	25*	27	19*	11*	8
	L11	4	12	16	11	11	9	10	18	7	3	10
Red-vented	33*	36*	32*	51	10*	20	18	15*	13*	16*	20*	14*
	95	68	73	43	32	28	22	31	35	38	35	44
Nuuanu Valley												
Red-whiskered	50*	17	25*	23	34*	25*	28*	32*	34*	27*	17*	22*
	12	18	10	21	13	4	9	6	7	8	5	8
Red-vented	34	30	20	17	36	18	23	18	19*	23	20	18
	29	18	16	14	23	26	24	18	39	21	27	15

* $P < 0.05$.

tioning within their native ranges (Ali and Ripley 1971). Vijayan (1975) examined their ecological isolation in India and concluded that distributional patterns were determined by habitat characteristics. According to those authors, distributions of red-whiskereds and red-venteds in India exhibited a high degree of overlap, with both species occurring in agricultural and residential areas and in scrub jungle. However, the red-whiskered was found predominantly in wet habitats from 500–2000 m elevation, whereas the red-vented occurred predominantly in dry habitats from sea level to 1500 m.

Based on the above discussion and on observations made during our initial surveys of bulbul distributions on Oahu, we generated two hypotheses. These were: (1) the Red-whiskered Bulbul occurs predominantly in the upper wet portions of Manoa and Nuuanu valleys; and (2) the Red-vented Bulbul occurs predominantly in lower elevation, drier habitats near the mouths of Manoa and Nuuanu valleys. We tested these hypotheses, using data from the monthly transect censuses in Manoa and Nuuanu valleys.

Bulbuls on Oahu demonstrated habitat preferences similar to bulbuls in India and these differences may be responsible for their present distributions. Census results from the transects confirmed that the Red-whiskered Bulbul occurred predominantly in the wet upper residential portions of Manoa and Nuuanu valleys. However, the few observations from the wet exotic forest above the transect included few or no red-

whiskereds. These observations need further corroboration (and are under continuing investigation), but suggest that red-whiskered densities decreased rapidly in all directions outward from the wet urban residential habitat in upper Manoa and Nuuanu valleys. Therefore, the preferred wet exotic residential habitat of red-whiskereds can be viewed as occurring on Oahu in a series of disjunct patches located at the heads of leeward valleys. Consequently, range expansion by the red-whiskered on Oahu has probably been impeded by difficulty in dispersal and colonization between habitat patches in the valley heads.

As predicted, the Red-vented Bulbul occurred predominantly in the lower half of Manoa Valley in drier habitats; however, in Nuuanu Valley, numbers of birds observed in the upper and lower halves of the transect did not differ significantly ($P > 0.05$). Results of the initial distribution survey and the transect counts showed a continuous distribution of the Red-vented Bulbul throughout residential portions of central Honolulu. Highest concentrations were observed in areas at low elevations, such as lower Manoa Valley, the Fort Shafter area, and along the windward (northeast) coast. Although Red-vented Bulbuls were abundant in agricultural, residential, and kiawe (*Prosopis pallida*) scrub habitats along the north, east, and south coasts and throughout the central valley (see Fig. 2), their numbers decreased rapidly as one progressed up into the Koolau Mountains (Shallenberger 1978, this study) or the Waianae Mountains (this study).

High concentrations of red-venteds on Oahu were continuous, that is, they were not separated by areas of low concentration as were those of the red-whiskered. The highest numbers of red-venteds occurred in the lower elevations and drier portions of all valleys throughout Honolulu and along the windward coast. These habitats form a continuous belt around the perimeter of Oahu and through the center of the island, and thus have apparently served as a corridor for dispersal and range expansion of the Red-vented Bulbul on Oahu.

SUMMARY

Population growth and distributional patterns of Red-whiskered (*Pycnonotus jocosus*) and Red-vented (*P. cafer bengalensis*) bulbuls were examined from their introductions to Oahu in the mid-1960s to the present. Population growth rates for the two species did not differ significantly ($P > 0.05$). The red-whiskered was observed only in the central Honolulu area, primarily in wet, exotic, residential habitats above 150 m elevation; whereas, the red-vented was observed in most habitats below 200 m island-wide. These observed differences in habitat preference were quantified and found to differ significantly ($P < 0.05$) using 12 monthly transect censuses in Manoa and Nuuanu valleys. Differences in the distributions of the two bulbuls can be explained as a result of differences in habitat preference. The wet, exotic, residential habitat preferred by the red-whiskered is of restricted size and occurs in disjunct patches, thus limiting the spread of the Red-whiskered Bulbul across Oahu. Lower

elevation, drier habitats form a continuous belt around the perimeter of Oahu and through the center of the island and thus, have apparently served as a corridor for dispersal and range expansion of the Red-vented Bulbul on Oahu.

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